Monstrilloid Copepods: the Best of Three Worlds

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Abstract.—Monstrilloids are one of the most intriguing groups of copepods. Their complex life cycle represents the successful evolutionary outcome of dealing with three distinct kinds of habitat, viz., planktonic, benthic, and endoparasitic, each of which presents particular challenges that have been overcome by monstrilloids. These copepods combine a unique set of strategies and adaptations to complete their life cycle. The non-feeding planktonic adult phase lacks mouthparts and their antennules are fixed, thus limiting their swimming abilities but they compensate for this handicap by having powerful swimming legs and probably generate a very distinct hydrographic signal that may be useful in avoiding predators and allowing sexual recognition between adult males and females. Parasitizing exclusively on abundant, gregarious sessile or sedentary benthic organisms represents an advantage in that potential hosts can be found without the need for long-distance dispersal. The endoparasitic stages of monstrilloids are unique; after infection by an early planktonic nauplius, successive nauplioid stages feed on their own vitellum while developing feeding tubes to absorb nutrients from their hosts. They grow within the host's body as successive copepodite stages that are contained in a protective sheath. Preadult individuals exit through the host body wall causing significant host damage or death, behaving in these instances as parasitoids. The diversity of the group appears to be underestimated, and extensive geographic areas remain completely unknown for this group of copepods. More effort will be required to advance our knowledge of monstrilloid diversity and biology that are yet to be revealed.

In this contribution, I intend to explore the vicissitudes experienced by monstrilloid copepods in the three different types of habitat they frequent: the plankton, the benthos, and as endoparasites, the bodies of their hosts. Along the way I will also present an overview of the group. The name of this group is striking; are they really monsters? There are many kinds of monsters, but the basic concept implies the possession of unusual, extraordinary characters. Of course, many highly modified copepods would qualify as such in this concept. For the American zoologist James D. Dana (1849) monstrilloids were indeed monsters, and when he described the genus *Monstrilla* and emphasized their lack of mouthparts ("...*maxillis pedibusve non munitus*"), it was clear that he was impressed by these odd copepods. He may have asked himself how they feed or wondered about their life cycle, because for him this feature qualified as a monstrosity. This character in monstrilloids has been a source of puzzlement and doubt ever since, because it constitutes an obstacle to the study of evolutionary relationships. As Huys and Boxshall (1991) fully recognized, this lack of mouthparts makes any fruitful analysis of monstrilloid appendage
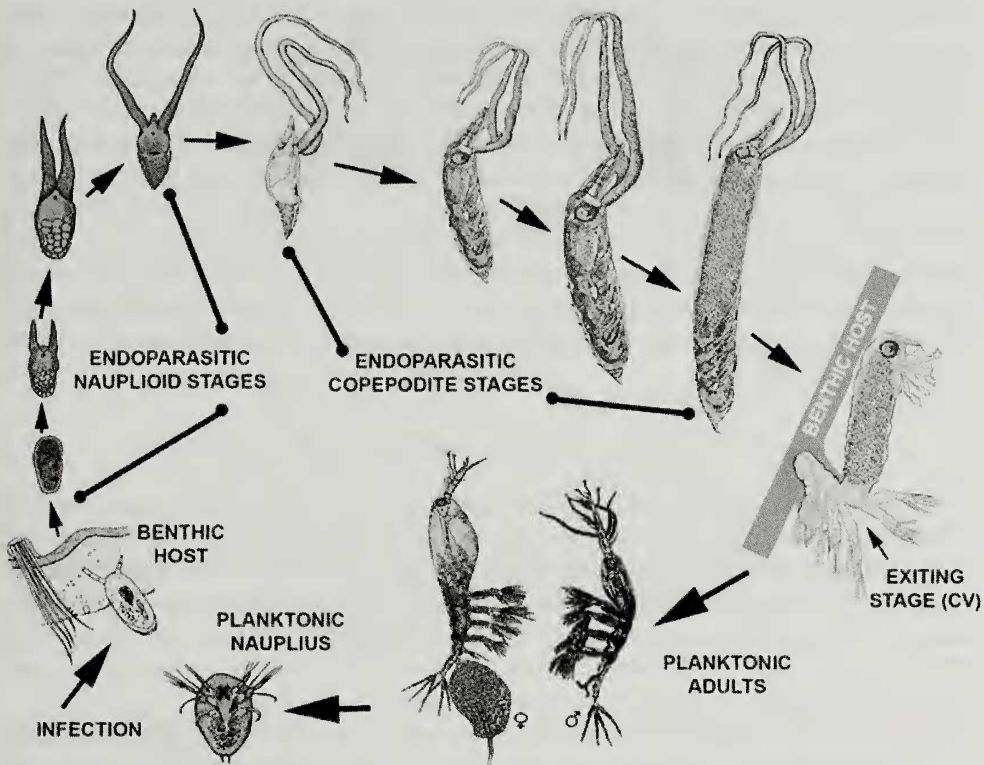

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Fig. 1.   Generalized life cycle of the Monstrilloida (based on Malaquin 1901; Suárez-Morales et al. 2014; Huys 2014).

homologies elusive. The ancestral links of these copepods remain hidden, a challenging mystery.

The Monstrilloida comprises a peculiar lineage of protelean parasitic copepods. They are endoparasitic in marine benthic invertebrates during their postnaupliar and copepodite stages but also have basically two free-living, planktonic phases, an infective naupliar stage and exclusively reproductive adult (Fig. 1; Malaquin 1901; Suárez-Morales et al. 2014). So, they are known mainly from adult individuals that are captured during zooplankton surveys in coastal environments (Suárez-Morales 2011).

As is true for many other highly modified copepods, their general morphology can be described oxymoronically as a model of complex simplicity. The lack of feeding appendages in monstrilloids has urged researchers to find new characters and explore their taxonomic value. In two essential publications, Grygier and Ohtsuka (1995, 2008) have contributed much to achieve this. The monstrilloids are currently represented by five valid genera: *Monstrilla* Dana, 1849, *Cymbasoma* Thompson, 1888, *Monstrillopsis* Sars, 1921, *Maemonstrilla* Grygier and Ohtsuka, 2008, and the recently described *Australomonstrillopsis* Suárez-Morales and McKinnon, 2014.

The main taxonomic characters used to identify monstrilloids include their body shape and proportions, the antennule length, the presence and development of the eyes, the position of the oral papilla, and the number of caudal setae, this last being one of the genus-defining features (Suárez-Morales 2011, 2015). Other characters are related to the

antennule setation pattern, with more than 30 named setal elements in males and females. Also, the structure and setation of the female fifth leg and the male genital complex are important. Cephalic cuticular features are also useful and some are reminiscent of their endoparasitic life, such as the paired scars of their feeding tubes that remain in the adults.

Early studies of the biology of these copepods by French researchers (e.g., Giard 1896; Malaquin 1901) revealed part of the monstrilloid life cycle, and Giard (1896) recognized its complexity as a zoological challenge, "...*L'ethologie des Copépodes de la famille des Monstrillidae est un problème qui a vainement exercé la sagacité des zoologistes ....*" They have morphological, physiological, and behavioural adaptations to simultaneously thrive in all three of the above challenging environments. In this contribution I will provide some facts and ideas about the adaptive features they use to deal with the complications inherent to each of these ways of life.

Plankton

Sinking in the water column is one of the main problems that planktonic organisms face. Calanoid copepods, clearly the most successful group in the zooplankton (Bradford-Grieve et al. 2010) show effective adaptations to improve their buoyancy. These features include long, powerful antennules, remarkably well developed cephalic appendages armed with a number of extended setae, and a supply of lipids within the body (Visser and Jónasdóttir 1999; Schründer et al. 2014). Monstrilloids lack these advantages, but as we will see, they compensate for this with adaptive characters to survive in the plankton.

The monstrilloid antennules are usually equal to less than 45% of the total body length (i.e. combined length of the prosome and urosome). They are typically rigid, straight and anteriorly directed, with short muscles attached to a thick, diagonal band of cephalic muscles; they cannot be spread laterally. The antennules are 4-segmented in the females although some species have segments 3-4 or 2-4 fused as in several species of *Cymbasoma* (Suárez-Morales et al. 2006). In males, the antennules are 5-segmented, with a distal geniculation involving a single segment with a distinctive setation pattern (Huys et al. 2007).

The lack of mouthparts and antennules that are functional in locomotion highlights the role of thoracic leg propulsion in monstrilloids during their free-living planktonic phase. As with other planktonic copepods (Kiørboe 2011), adult monstrilloids have four pairs of biramous swimming legs. Both rami are always three-segmented, with a conservative ancestral armature (Huys and Boxshall 1991). These legs have a strong set of muscles and long, setulated setae, certainly an efficient gear for propelling themselves in the water column during their short planktonic phase. They have the necessary swimming power but with their rigidly fixed antennules how do they manage to navigate while seeking a mate in the three-dimensional pelagic realm?

Efficient swimming is a matter of decreased water resistance. Calanoid copepods show different kinds of displacements, including a gliding movement created mainly by mouthparts and antennae, and power swimming, in which the lateral sweep of the flexible antennules is strong and completed by that of the swimming legs (Jiang and Kiørboe 2011). This makes calanoids efficient swimmers indeed. Each of these two swimming modes has a differential hydrodynamic signature. Lacking the benefits of the large antennules and antennae, it is speculated that monstrilloids use their rigid, straight antennules as a form of streamlining to maintain an efficient, straight path during their displacements in the water column. They appear to be designed to obtain the best hydrodynamic advantage from the leg-based propulsion.
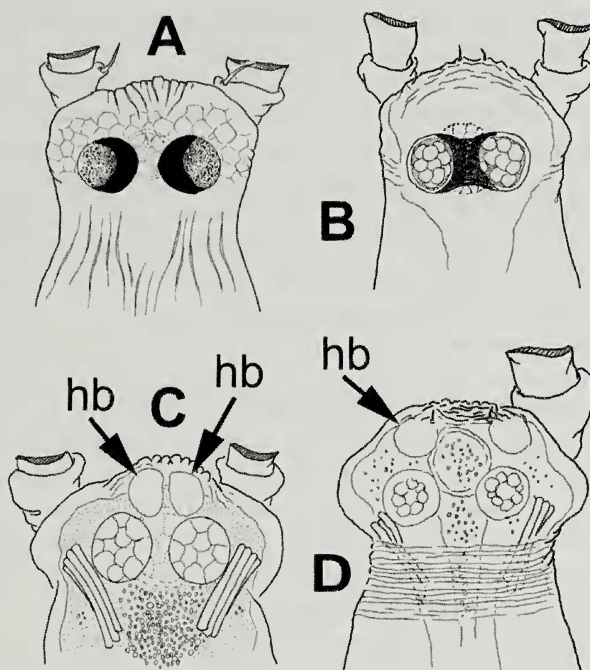
Fig. 2. Eye development in monstrilloid copepods and position of hyaline bodies (hb) with respect to ocelli. (A) Eyes with strongly pigmented inner half, without hb; (B) Eyes medially conjoined by pigmented area, without hb; (C) Eyes unpigmented, with hb on medial position; (D) Eyes unpigmented, with hb separate.

From the analysis of a series of video recordings taken by Dora Pilz (University of Miami) involving two monstrilloid species, including *Cymbasoma davisi* Suárez-Morales and Pilz, 2008, it was determined (pers. obs.) that monstrilloids display a weak hopping movement with a basically continuous straight trajectory that contrasts with the skillful swimming displayed by other copepods. A typical leg beat involves a rapid backward stroke of the four swimming legs in a 4-1 sequence (e.g., first swimming stroke of leg 4, last of leg 1), as described for other planktonic copepods (Jiang and Kiørboe 2011). A flap of the urosome can add strength to the leg movement. It is speculated that this kind of swimming creates a very different, probably weaker hydromechanical disturbance signal in the surrounding water than that generated by calanoids; this greatly reduced signal could represent an advantage to avoid alerting potential predators that are adapted to perceive planktonic copepods as prey.

As in many other copepods, the nauplius eye of monstrilloids consists of one median and two lateral ocelli, each within a pigment cup. The medial eye can be larger than the lateral ocelli cups or about the same size; in some cases, the eyes are small and inconspicuous, lacking pigmentation (Fig. 2C, D). The distances between the eyes, and the pigmentation pattern and intensity, are variable (Fig. 2). This kind of complete and strong eye development is comparable to that of holoplanktonic forms (i.e., calanoids) and presumably it constitutes an additional tool to survive in the plankton. In some species, a pair of lens-like "hyaline bodies" (hb in Fig. 2) is located near the lateral cups. Their function is unknown,

but they readily bring to my mind the cuticular lenses of pontellid calanoids, which are sensitive to light and polarization (Manor et al. 2009).

Finding a mate is essential for copepod reproduction. Detection of potential mates by pheromones has been widely documented, and distinctive hydromechanical signatures have also been reported (Strickler 1998; Kiørboe 2007, 2011). For the non-feeding adult monstrilloids with a very limited time in the plankton, finding a prospective mate in the shortest period possible is their priority. Their mating behaviour remains largely unknown, but it probably includes the tracking of unique hydromechanical cues produced by females or males, not primarily the tracing of pheromones. This set of adaptive behaviours and characters increases the chances of a successful planktonic stage.

The highly fecund free-spawning calanoids lack parental care (Titelman et al. 2007), whereas egg-carrying forms display a certain level of parental care. At certain conditions, some planktonic species show increased fecundity levels (Holste and Peck 2005). Monstrilloids lack egg sacs but they possess ventral ovigerous spines that comprise two slender, spiniform structures of variable length in different species. Eggs remain attached to these structures by a mucous substance. In *Maemonstrilla* the ovigerous spines are anteriorly directed, set close and parallel to the body axis. This peculiar pattern, together with the remarkably wide intercoxal sclerites of legs 1–4, enables these copepods to provide extended parental care by subthoracic brooding (Grygier and Ohtsuka 2008). This is yet another adaptation, not known in other planktonic copepods, to improve the survival of their offspring in the planktonic realm.

Mass aggregations of planktonic copepods have been reported for many reef-related species and are deemed as an adaptive behavior to enhance the likelihood of mate encounters (Titelman et al. 2007). Usually, monstrilloids are caught in numbers of 2 or 3 if at all, but they can swarm; in a Caribbean coral reef area more than 800 individuals of a single species were collected during one ordinary plankton trawl. They aggregate at dusk, thus contrasting with daylight swarming of planktonic copepods (Suárez-Morales 2001). This implies that monstrilloids probably avoid predators by undertaking vertical migration and remaining near the bottom, closer to their potential benthic hosts. Adaptive migratory patterns have been also proposed as planktonic copepod strategies to avoid predation in the water column (Pasternak et al. 2006).

Benthos

Monstrilloids are known as parasites of the benthic macrofauna, including several families of sessile and errant polychaetes, gastropod and bivalve molluscs, and even sponges (Huys et al. 2007; Suárez-Morales 2011) (Table 1). So, in this sense, the period in which monstrilloids live inside these benthic invertebrates, they are part of the hyperbenthic and epibenthic community (Gray and Elliott 2009), just as the epifauna and epiflora (i.e., symbiotic organisms living attached to the macrofauna), but inside the body.

The monstrilloid hosts tend to be sessile or sedentary and gregarious marine invertebrates, something that should favor maintenance of the local character of parasite faunas. Parasites are able to profoundly transform the community structure, behaviour, and reproduction of benthic invertebrates (Mouritsen and Poulin 2002), but the effect of monstrilloids on the population dynamics of their hosts has not been studied. It is likely that the monstrilloid life cycle takes advantage of various factors inherent to the benthic community: 1) the tendency of these benthic groups to have aggregate populations (Anderson 2008), and the concomitantly greater chance of larvae encountering the host

Table 1. Recorded hosts of the Monstrilloida.

Phylum/Class	Family	Species	Monstrilloid	Reference
Porifera	—	—	Monstrilloid	Huys et al. (2007)
Mollusca				
Gastropoda	Pyramidellidae	*Brachystomia scalaris* (McGillivray, 1843)	*Monstrilla helgolandica* Claus, 1863	Pelseneer (1914); Gallien (1934)
	Vermetidae		Monstrilloida	Huys et al. (2007)
	—		Monstrilloida	Boxshall and Halsey (2004)
Bivalvia	Mytilidae	*Perna perna* L., 1758	*Monstrilla* sp.	Suárez-Morales et al. (2010)
Annelida				
Polychaeta	Capitellidae	*Capitella capitata oculata* Hartman, 1961	*Monstrilla capitellicola* Hartman, 1961	Hartman (1961)
	Serpulidae	*Salmacina dysteri* (Huxley, 1855)	*Cymbasoma danae* (Malaquin, 1901) (as *Haemocera danae*)	Malaquin (1901)
		Filograna implexa Berkeley, 1835	*Monstrillopsis filogranarum* (Malaquin, 1901) (as *H. filogranarum*)	Malaquin (1901)
		Salmacina setosa Langerhans, 1884	*Cymbasoma roscovita* (Malaquin, 1901) (as *Haemocera roscovita*)	Malaquin (1901)
		Serpula vermicularis L., 1767	Monstrilloida	Huys and Boxshall (1991)
		S. dysteri and *F. implexa*	Monstrilloida	Nishi in Grygier (1995)
	Spionidae	*Polydora ciliata* (Johnston, 1938)	*Cymbasoma germanicum* (Timm, 1893)	Malaquin (1901)
		Dipolydora giardi (Mesnil, 1893)	*C. germanicum*	Giard (1895) (as *Thaumaleus* sp.); Malaquin (1901); Caullery and Mesnil (1914)
	Syllidae	*Exogone* Örsted, 1845	Monstrilloid	Caullery (1908)
		Syllis gracilis Grube, 1840	*Cymbasoma malaquini* (Caullery and Mesnil, 1914) (as *Haemocera*)	Caullery and Mesnil (1914)
		Haplosyllis sp.	*Monstrilla* sp.	Suárez-Morales et al. (2014)

within a reduced spatial scale; 2) monstrilloids are more frequently found as parasites of polychaetes, deemed as the most abundant group in the benthos (Dean 2008; Gray and Elliott 2009); 3) the sessile or sedentary (moving within one place, not fixed or with weak dispersal abilities) nature of their hosts enables monstrilloids to remain linked to basically the same host populations and also to suitable hydrographic conditions including tidal currents. As monstrilloids inhabit near-shore coastal habitats, including docks, they use retention areas that are locally generated by microscale dynamics to remain close to the benthic community and to their potential hosts (Suárez-Morales and Pilz 2008). There are relatively few records of monstrilloids in fully oceanic waters. Together with their weak dispersal abilities, their link to the benthic communities may also explain the presumed restricted distributional patterns of the Monstrilloida (Suárez-Morales 2011).

Endoparasitic

Monstrilloids are impressive parasites, and when they invade the host they condemn it. A free-swimming lecithotrophic naupliar stage is recognized as the infective stage (Grygier and Ohtsuka 1995). The antennae and claw-bearing mandibles are used to efficiently attach to and penetrate the host body wall (Fig. 1); the cephalic end of the nauplius penetrates first and then the antennae sway back and forth on the host integument to complete the invasion (Malaquin 1901).

Once inside the host, the endosymbiont nauplius starts to develop feeding tubes, but probably keep living on its vitellum for some time during 3-4 stages I call "nauplioid" herein. When the feeding tubes become functional and begin to extract fluids from the host, the larvae become truly endoparasitic. At these early stages the copepod is covered by a thin membrane around the body (Pelseneer 1914; Suárez-Morales et al. 2014: Fig. 9). It is likely that there are at least three copepodite stages and they can have 1-3 pairs of feeding tubes (Malaquin 1901; Caullery and Mesnil 1914; Suárez-Morales et al. 2014). Suárez-Morales et al. (2014: Fig. 9A) shows a CIII individual extracted from its polychaete host with the membrane still around its body. The same specimen (Suárez-Morales et al. 2014: Fig. 9B, C) shows two antero-ventral feeding filaments that are formed by tubes with small bulbous structures that are speculated to represent different molts. The bulbous structures lead to terminal pads that appear to be connected to the inner tissues of the host to extract its body fluids.

Usually, parasites found in the polychaete host are lodged along the main axis with their ventral surface facing the digestive system of the host, with the cephalic end pointing towards the posterior part of the host body. When more than one parasite is present they tend to lodge on opposed positions, both facing their ventral surface to the host digestive tube. Infection by monstrilloids can be detected as nodules on the mantle of molluscs (Suárez-Morales et al. 2010) or growing swellings of the body surface of polychaetes (Suárez-Morales et al. 2014). The effects of the parasite include intense haemocytic infiltration, swelling, and castration (Malaquin 1901; Suárez-Morales et al. 2010).

At the last juvenile phase, monstrilloids quite dramatically leave the host, breaking through its body wall by first exposing the urosome (Suárez-Morales et al. 2014: Fig. 11A, B) and then moving the cephalothorax until the legs and the antennules are completely withdrawn from the host body (Malaquin 1901). Caullery and Mesnil (1914) reported a different exiting sequence, with the middle of the body emerging first, followed by the cephalosome and finally the urosome. The final separation from the host is probably not immediate and the copepod probably remains partially attached for a while; the remains of

Table 2. Number of species of each monstrilloid genera reported from coastal waters of five continents.

	Cymbasoma	Monstrilla	Monstrillopsis	Maemonstrilla	Australomonstrillopsis	Total
Europe	15	14	5	—	—	34
Asia	14	13	2	9	—	38
America	20	20	9	—	—	49
Australia	25	1	3	4	1	34
Africa	4	7	—	1	—	12

the sac and the feeding tubes remain inside the host (Caullery and Mesnil 1914). According to Malaquin (1901), the host may recover after the parasite exits its body. In the mytilid mollusc *Perna perna*, the copepod does not kill the host (Suárez-Morales et al. 2010), but it does in other instances (Suárez-Morales et al. 2014). So, the boundary between being parasites and parasitoids is not quite clear in reference to monstrilloids; the outcome of the symbiosis may depend on the relative size of the host and also on the number of parasites in the individual, which is also related to their position and space arrangement within the host (Malaquin 1901). According to Malaquin (1901) and Caullery and Mesnil (1914), the sex of the parasite is determined by the number of individuals infecting a host. When 2-3 monstrilloids develop in the same host individual, they all develop into males. By contrast, females arise from hosts with a single parasite in the body.

Diversity and Distribution

Because of their morphological simplicity, incomplete descriptions, a long history of nomenclatural problems (Grygier 1994a; Suárez-Morales 2011; Grygier and Suárez-Morales submitted) and the difficulties in linking males and females of a particular species, the diversity of monstrilloids is far from being accurately known (Suárez-Morales 2011, 2015), and is certainly underestimated. Only a few years ago, just a couple of species of *Cymbasoma* were known from all of Australia but a recent revision of new material revealed a much higher diversity (i.e., 25 species) (Suárez-Morales and McKinnon 2014). Based on a revision of the available data and recent additions in 2017 (Suárez-Morales et al. 2017), up to 154 nominal species are recognized: 72 of *Cymbasoma*, 57 of *Monstrilla*, 14 of *Monstrillopsis*, 11 of *Maemonstrilla*, and 1 of *Australomonstrillopsis*. As it is likely that more undescribed species and probably new genera will result from ongoing surveys of the monstrilloid fauna from Australia, Canada, and Korea (Jeon et al. 2018), their true diversity is yet to be revealed.

How is this diversity distributed among the continents? Table 2 shows the distribution of the known diversity of the group. As stated by Suárez-Morales (2011), it is remarkable that several nominal species are reported in all the continents. This is a group of pseudo-cosmopolitan species, and many of their records are suspect as a result of the problems mentioned before. Here I show in parentheses the number of species that are actually known or are assumed to be subsumed under each of these names: *Cymbasoma rigidum* Thompson, 1888 (3), *C. longispinosum* (Bourne, 1890) (6), *Monstrilla grandis* Giesbrecht, 1891 (3-4?), *M. helgolandica* Claus, 1863 (2-3), and *Monstrillopsis dubia* (Scott, 1904) (4), but there are probably many more (Grygier 1994b; Suárez-Morales 2006; Üstün et al. 2014).

The genus *Cymbasoma* is slightly less diverse in Europe than in the Americas; it appears to be most diverse in Australia (Suárez-Morales and McKinnon 2016). A similar

situation is found for *Monstrilla*, which is less species-rich in European waters than it is in the Americas, where extensive areas (e.g., the South American Pacific coast) remain unexplored for this genus, without a single record. Knowledge of this genus is expanding in the Indo-Pacific region, mainly in Japan and Korea (Chang 2014; Jeon et al. 2018), but extensive unstudied areas still remain. Analysis of the Australian monstrilloids is still an ongoing project, and their numbers there could grow, especially for *Monstrilla*.

The less species-rich genera show a similar pattern. America has the highest number of species of *Monstrillopsis*, followed by Europe and Australia. *Monstrillopsis* tends to occur in temperate and cold latitudes, and only three species have been recorded from fully tropical areas (Suárez-Morales 2006; Suárez-Morales and McKinnon 2014). *Maemonstrilla* is largely restricted to the Indo-West Pacific. Most species have been found in Japanese coral reef areas and in Australian waters but some are known from India and Indonesia (Grygier and Ohtsuka 2008; Suárez-Morales and McKinnon 2014). *Australomonstrillopsis* is endemic to Australia (Suárez-Morales and McKinnon 2014). Africa is clearly a treasure-box of monstrilloid diversity yet to be opened.

Phylogeny

As a group associated with different types of habitats involving distinct life modes, monstrilloids have a unique mixture of characters that are shared with various other groups of copepods, and their phylogenetic relations within the Copepoda have been a matter of discussion for over a century. A common ancestor with the Phyllodicolidae, a cyclopoid family parasitic on polychaetes, was proposed by Gotto (1961). Later on, monstrilloids were positioned by Huys and Boxshall (1991) as a sister taxon of the order Siphonostomatoida. A phylogenetic analysis by Huys et al. (2007) suggested a common ectoparasitic ancestor for monstrilloids and caligiform taxa, with a host shift from pelagic vertebrates (teleosts) to sessile benthic invertebrates coincident with the divergence of these two lineages, and also resulted in the proposed demotion of monstrilloids to a family of the order Siphonostomatoida. To the contrary, a recent, comprehensive analysis of the copepod orders with upgraded molecular standards (Khodami et al. 2017) supports the status of the Monstrilloida as a monophyletic order forming a sister-group with the siphonostomatoids in a single clade. This is also coincident with a COI-based analysis performed by Su et al. (2016) for the Korean planktonic copepods. The phylogeny of the genera within the Monstrillidae has not been explored but it is hypothesized that, because of the presence of significant reductions (i.e., urosome segmentation, number of caudal setae, fifth leg armature), *Cymbasoma* could be revealed as the most derived genus and *Monstrilla* the most primitive, but a full analysis would be needed to support this.

There are several exclusive characters of the Monstrilloida including: 1) an infective nauplius vs. infective copepodites in other parasitic groups (Ho et al. 2003; Ohtsuka et al. 2018); 2) naupliar mouthpart structure (Grygier and Ohtsuka 1995); 3) the unique endoparasitic nauplioid/copepodite development pathway (Huys 2014; Suárez-Morales et al. 2014); and 4) distinctive leg development with early completion (at stage CIII) of the setal armature of legs 1-4, loss of one exopodal seta of leg 1 at CIV, and full development of leg 1 ENP at CIII (Suárez-Morales et al. 2014). Some other characters are shared with selected copepod taxa. For example, the lack of mouthparts and antennule structure and function in non-feeding adults are shared with members of the cyclopoid family Thaumatopsyllidae. Furthermore, the dual mode of parasitism (endo vs. ectoparasitic cycle) and the use of invertebrate benthic hosts are also shared by many siphonostomatoid and

cyclopoid taxa. Monstrilloids are clearly a compact, well defined but intriguing lineage still posing many, many questions we have not been able to solve.

In 1707, the Swiss diluvianist Johannes Scheuchzer published his *Complaints and Claims of the Fishes*, in which he gave voice to the fish; they claimed to be witnesses of the Universal Flood but also complained about the human misinterpretation of their fossils. So, I'm going to do the same here and speak out on behalf of monstrilloids: "...*we have been able to survive in three really harsh worlds and here we stand, probably against all odds. Today, with our raised rigid antennules, we claim for understanding and more research efforts from copepodologists. We, the monstrilloids claim our place in the world!!*"

Other copepod groups make similar requests, but there are so many aspects of monstrilloid ecology, biology, genetics, behavior, and taxonomy that we do not know or understand as yet (see Suárez-Morales 2011). There remains for us both an opportunity and a continuous challenge: research on this awesome group of crustaceans will always be a canvas on which we can keep spreading our science, our art, copepodology.

Acknowledgments

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